

COLOUR DISCRIMINATION IN THE POLLINATION OF *PORTULACA GRANDIFLORA* HOOK., BY *APIS MELLIFERA* L.

D. J. MOGFORD

(Department of Plant Sciences, Rhodes University, Grahamstown)

ABSTRACT

Few data are available on colour discrimination by honeybees during actual pollination. The present work indicates that in *Portulaca grandiflora* the purple flowers are discriminated against, relative to yellow and orange flowers.

UITTREKSEL

KLEURONDERSKEID BY DIE BESTUIWING VAN *PORTULACA GRANDIFLORA* HOOK. DEUR *APIS MELLIFERA* L.

Min gegewens is beskikbaar oor die kleurvoorkeur van heuningbye gedurende bestuiwing. Die huidige werk dui daarop dat by *Portulaca grandiflora* daar teen die pers blomme gediskrimineer word ten gunste van geel en oranje blomme.

INTRODUCTION

In an insect-pollinated species, variation in flower colour is a particularly significant form of variation. This is because the evident adaptive significance of flower colour in relation to insect pollination suggests certain of the factors which may underlie the maintenance of the variation. This contrasts with most other forms of variation, such as the vast reserves of isoenzymic polymorphism revealed by electrophoretic studies, in which the factors maintaining the variation remain almost completely unknown.

The various ways in which flower colour variation may be maintained by pollination have been reviewed in detail by Mogford (1978). In outline, it is necessary first to distinguish between instances of polymorphisms and other forms of stable variation, and instances of variants maintained merely by recurrent mutation and removed by selection (Ford, 1975). Of the former categories, the principal consideration is whether certain of the types are subject to preferential pollination, in which case three types of situation may be distinguished:

- (a) those situations maintained by some advantage which accrues from the favoured type being visited first;
- (b) those situations where the overall level of pollination of the population is increased by the favoured types attracting higher numbers of pollinators, or encouraging foraging for longer periods; and
- (c) those situations where the differences in attractiveness vary between pollinating species, thereby providing a degree of divergence in pollinator between the

colour types. This is perhaps the most significant situation, in that the flower colour variation is acting as a means of cleaving the population into segregates between which there occurs limited gene flow. Accordingly, the variation is acting as a medium for sympatric evolutionary divergence with respect to the whole gene pool.

Records of colour discrimination during pollination are therefore of interest. Instances have been recorded in *Lantana camara* (Dronamraju, 1960), *Leavenworthia crassa* (Lloyd, 1969), *Raphanus raphanistrum* (Kay, 1976), *Cirsium palustre* and *Anagallis arvensis* (Mogford, 1972, 1974 a, b, 1978). However, few data are available on the discriminatory responses of the honeybee, *Apis mellifera* L., during pollination. The present work was therefore designed to study the possible occurrence of colour discrimination in the pollination of the rose moss, *Portulaca grandiflora* Hook., by honeybees.

MATERIAL AND METHODS

Observations were conducted during February and March, 1978, on a large bed of evenly spaced, single-flowered plants of *P. grandiflora* in Grahamstown Botanic Garden. The population consisted of a majority of purple-flowered plants, together with smaller numbers of red, yellow, and orange plants. No differences were observed between the colours except in pigmentation.

The population was visited almost exclusively by pollen-collecting honeybees. Foraging commenced when the bed was illuminated by direct sunlight, at about 09h00, at which time the flowers opened. The flowers remained open for only about three hours, despite continued illumination by direct sunlight. Competition for pollen was most intense among newly-opened flowers.

Observations were conducted over 14 mornings. In each case observations were restricted to within a marked area of 5 square metres. The number of flowers of each type within the area was counted prior to each period of observation, following which the visits of bees to flowers within the area were observed and classified with respect to colour. Individual bees were followed for as long as possible in order to reduce human bias in the choice of plants. A different marked area was used for each period of observation, in order to reduce the effects of any local differences in plant size.

For each period of observation, the number of flowers of each colour present within the plot, and the number of each colour visited by the honeybees, were recorded. Two analyses were used to determine the type of discrimination afforded to each colour:

- (a) Comparisons were performed, using χ^2 , of the observed and expected number of flowers of a particular colour visited. These tests were performed separately for each colour versus the other colours combined, in each period of observation.

(b) Considering the observations as a whole, χ^2 tests were used to compare the total number of times each colour was preferentially visited, to the total number of times the colour was discriminated against. These comparisons were based solely on the types of discrimination indicated by the percentage values for occurrence and visits, regardless of the individual significance of these values when considered per period of observation. The method therefore provided a cumulative measure of discrimination with respect to each colour.

RESULTS

The results of analysis (a) are shown in Table 1, and those of analysis (b) in Table 2.

TABLE 1.
Flower colour and bee visit ratios for *P. grandiflora*.

Plot	Flower Colour Ratio					Visits Ratio					Discrimination Probability			
	P	R	Y	O	n	P	R	Y	O	n	P	R	Y	O
1	70.2	0.0	11.9	17.9	84	65.2	0.0	13.6	12.2	66	NS	—	NS	NS
2	75.8	3.0	12.1	9.1	66	71.3	2.8	12.0	13.9	216	NS	NS	NS	NS
3	63.0	9.8	2.2	25.0	92	55.6	12.6	5.9	25.9	135	NS	NS	*	NS
4	68.1	9.0	16.1	6.8	279	56.4	8.3	16.5	18.8	133	(**)	NS	NS	***
5	51.7	14.8	5.4	28.1	203	42.0	17.8	4.0	36.2	174	(*)	NS	NS	*
6	53.6	36.0	10.4	0.0	125	52.8	31.8	15.3	0.0	176	NS	NS	NS	—
7	54.0	36.5	3.8	5.7	211	43.4	38.0	8.5	10.1	129	(*)	NS	**	*
8	50.4	45.7	3.9	0.0	129	43.7	49.2	7.0	0.0	199	NS	NS	NS	—
9	49.0	34.8	14.8	1.3	155	37.8	35.7	21.0	5.6	143	(**)	NS	NS	***
10	64.0	15.4	2.2	18.4	136	58.7	17.5	7.3	16.5	206	NS	NS	***	NS
11	60.9	15.4	0.6	23.1	156	37.6	15.4	1.7	45.3	117	(***)	NS	NS	***
12	52.3	34.6	2.0	11.1	153	55.6	26.6	6.5	11.3	124	NS	NS	**	NS
13	75.8	3.0	12.1	9.1	66	70.7	3.0	12.0	14.3	133	NS	NS	NS	NS
14	70.8	8.8	4.4	16.2	68	44.8	11.9	11.9	31.3	67	(***)	NS	**	**

Ratios listed as percentage values based on sample size n.

Probability values calculated as described in text, analysis (a).

Unbracketed probability values indicate colours discriminated against.

* = significant at 5 % level
 ** = significant at 1 % level
 *** = significant at 0.1 % level.

Colour Type	Favoured	Neglected	Probability
Purple	1	13	(***)
Red	7	5	NS
Yellow	11	3	*
Orange	11	1	***

TABLE 2.

Cumulative analysis of pollination data for *P. grandiflora*. Values calculated as described in text, analysis (b). Probability values abbreviated as in Table 1.

Analysis (a) indicated discriminative visiting against the purple flowers, random visiting of the red flowers, and preferential visiting of the yellow and orange flowers. Thus, in six cases the purples were discriminated against, but in no case were they favoured; in contrast, the yellows were favoured five times, and never discriminated against, while the oranges were favoured six times, and never discriminated against.

The degrees of discrimination involved were small but quite consistent. Because of their individual smallness, analysis (b) was of particular value, and in fact confirmed the previous results, even to the extent of supporting the slight favouring of the orange over the yellow flowers suggested by the first analysis.

DISCUSSION

Several workers have shown the ability of honeybees to discriminate between colours in artificial experiments (Goldsmith, 1961). However, the colour responses of bees during actual foraging have been little studied, principally because fewer circumstances are available in which discrimination between flowers can be ascribed specifically to colour rather than floral structure or patterning. The result has been to emphasise the difficulty, pointed out by Meeuse (1961), of knowing the degree to which bees actually use the powers of colour discrimination which they evidently possess. The use of flower colour variants, however, obviates the difficulty of differences in floral structure, and provides a useful index of bee behaviour in nature.

As such, the results are of value in showing the capacity of *A. mellifera* for discrimination of this type. This is of interest since work on the flower colour polymorphism of *Cirsium palustre* indicated that, in an instance where honeybees were studied, they failed to show colour discrimination, unlike the general results obtained for *C. palustre* with bumblebees (Mogford, 1974b).

There are in fact two components which might lead to the type of result obtained in the present work: colour discrimination *per se*, and apostatic effects in bee behaviour which would result in over-visiting of the most frequent colour. Such apostatic effects are a consequence of the fact that, if "search-image" responses for a specific colour are elicited by successive, random visits to two or more flowers of that colour, then such responses would be elicited for the more common variety to an extent greater than that represented merely by its relative frequency in the population. The most common colours would therefore be preferentially visited in a response quite apart from any such based on colour preference *per se*.

However, in the present work, the most frequent colour was in fact discriminated against, indicating that search image responses were likely to be of minimal importance. The same conclusion was reached in the study of the pollination of *Cirsium palustre* by bumblebees, by a method based on a comparison of bee visit sequences with heterogeneity in the distribution of colour types within populations

(Mogford, 1972). The present results may therefore be taken as indicating actual colour preference *per se*.

It is less certain whether pollination effects underlie the maintenance of the flower colour variation in *P. grandiflora*. The wide range of colours present in garden forms—which includes variation from pure white to yellow, rose, scarlet, deep red and purple (Bailey, 1930)—is undoubtedly maintained by the process of disruptive selection for flower colour variants practised by cultivators of all decorative species.

However, orange-flowered plants are known to be present in appreciable frequency among the typical purple-flowered plants in natural populations of the species in its native Brazil (Bailey, 1930). It is therefore quite probable that the presence of both orange and purple flowers constitutes a stable polymorphism in nature.

ACKNOWLEDGEMENTS

The author wishes to thank Mr J. D. Cameron, of the Grahamstown Botanic Garden, for the provision of facilities, and Mr D. Gautier for assistance in the collection of data.

REFERENCES

- BAILEY, L. H., 1930. *The Standard Cyclopaedia of Horticulture*. New York: Macmillan.
- DRONAMRAJU, K. R., 1960. Selective visits of butterflies to flowers a possible factor in sympatric speciation. *Nature, Lond.* **186**: 178.
- FORD, E. B., 1975. *Ecological Genetics*. London: Chapman and Hall.
- GOLDSMITH, T. H., 1961. The colour vision of insects. In: McElroy, W. D., and Glass, B. (eds.), *Light and Life*. pp. 771–793. Baltimore: John Hopkins.
- KAY, Q. O. N., 1976. Preferential pollination of yellow-flowered morphs of *Raphanus raphanistrum* by *Pieris* and *Eristalis* species. *Nature, Lond.* **261**: 230–232.
- LLOYD, D. G., 1969. Petal colour polymorphism in *Leavenworthia* (Cruciferae). *Contr. Gray Herb. Harvard* **198**.
- MEEUSE, B. J. D., 1961. *The Story of Pollination*. New York: Ronald.
- MOGFORD, D. J., 1972. *The Ecological Genetics of Flower Colour Variation in Cirsium palustre* (L.) Scop. D. Phil. thesis. Oxford: University of Oxford.
- MOGFORD, D. J., 1974a. Flower colour polymorphism in *Cirsium palustre*. 1. *Heredity* **33**: 241–256.
- MOGFORD, D. J., 1974b. Flower colour polymorphism in *Cirsium palustre*. 2. Pollination. *Heredity, Lond.* **33**: 257–263.
- MOGFORD, D. J., 1978. Pollination and flower colour polymorphism, with special reference to *Cirsium palustre*. In: Richards, A. J. (ed.), *The Pollination of Flowers by Insects*. Linnean Symp. Ser. No. 6. London and New York: Academic Press.